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FACTORS AFFECTING POPULATIONS OF SOCIAL WASPS, *VESPULA* SPECIES, IN ENGLAND (HYMENOPTERA)

By G. Fox-Wilson, N.D.H., F.R.E.S.

(*R.H.S. Laboratory, Wisley, Surrey*).

The purpose of this paper is to discuss in some detail certain factors considered to be directly and indirectly concerned with an abundance and scarcity of social wasps, *Vespula* species. It is based upon observations made in the Royal Horticultural Society's Gardens at Wisley.

Records have been kept at Wisley for a period of 25 years (1921–1945) on the number of nests which occurred in an area of some 100 acres—the sites of which for the past six years have been plotted (fig. 1). The wholesale destruction of nests within this area is necessary to avoid injury to the collection of grapes in the vineries and to the National Collection of apples, pears and plums. The severest damage was done to grapes in 1939 when, despite a small over-abundant population only (fig. 2), there occurred a massed assemblage of wasps in the vineries during August and September of that year.

No attempt had been made to correlate wasp abundance with climatic and other factors until the publication of a paper by Beirne (1944), in which he expounded the theory that the limiting factor is one of spring rainfall which operates chiefly in April, May and June. Considerable interest was aroused by the publication of this paper, and opinions were expressed by other entomologists (Scott 1945, Walsh 1945, and Latter *in litt.*) on the theory put forward. There was some, but not complete, agreement with the conclusions reached by Beirne.

After close consideration had been given to the factors concerned with seasonal abundance of wasps, it was apparent that the problem was one of some complexity. It would appear, however, that the factors concerned with climate and, in particular, with spring rainfall, are undoubtedly by far the most important and probably the chief ones concerned. It is doubtful whether long-range forecasting of wasp abundance is yet possible.

The Wisley records show that each season of abundance is generally followed immediately by one of scarcity, and this is followed by a season of abundance (fig. 3). It will be noted, however, that two or more seasons of scarcity and low populations (*e.g.* 1931–34) are followed by an over-abundance of wasps (*e.g.* 1935); again, the scarcities of the years 1936–38 were followed by an abundance in 1939. In some years (*e.g.* 1928, 1935, 1939 and 1942) the populations were high, irrespective of the spring rainfall (fig. 2, A). Thus, the accumulative effect of the limiting factor or factors is evident. It is seen that there is little constancy in wasp populations from one year to the next—such annual variations being striking and sufficient to warrant the term "Wasp Years" being given to those years of great abundance (*e.g.* 1928 and 1942). This term is used by Leclercq (1944) for the year 1942, when high populations were recorded not only from many districts in England, but also from the whole of Belgium, where serious injury was caused in orchards, shops and fruit stores

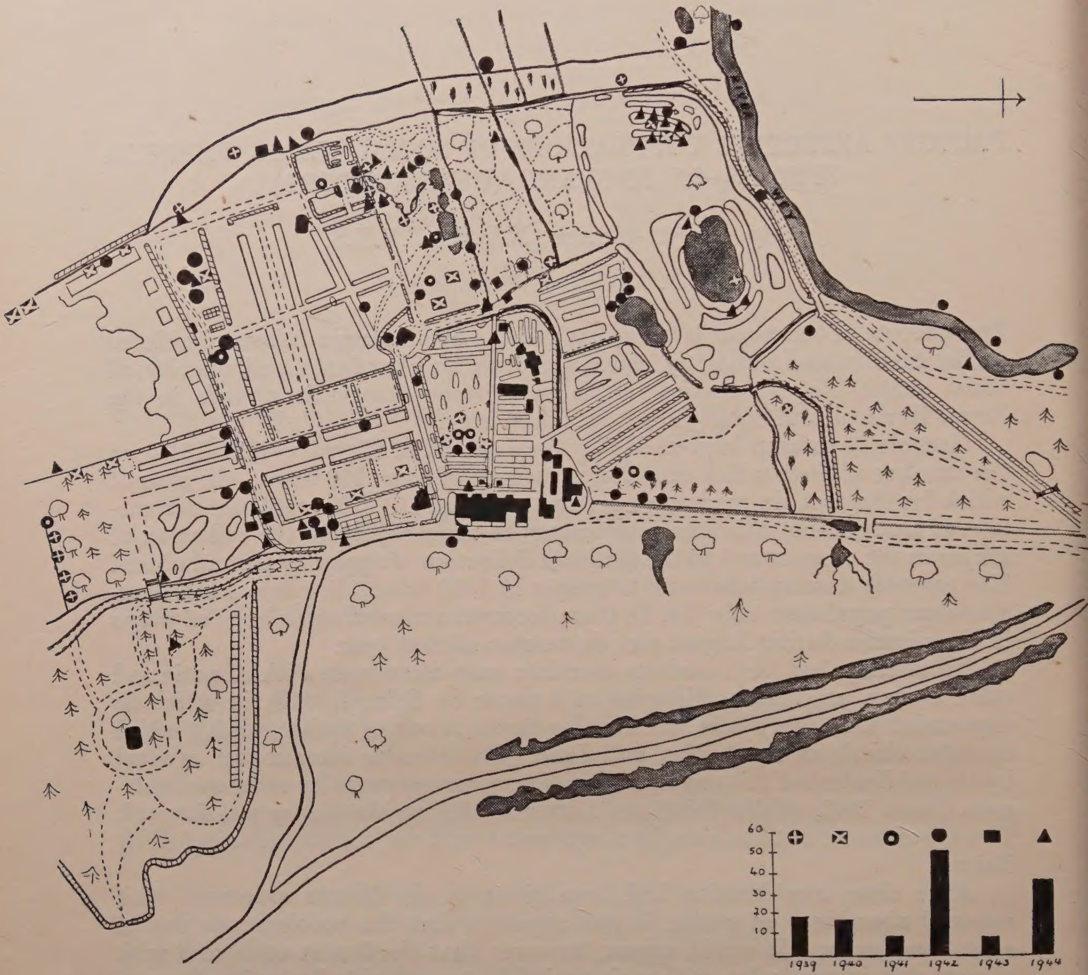


Fig. 1.—Plan of the Royal Horticultural Society's Gardens, Wisley, Surrey, indicating the sites of wasps' nests during the past six years (1939–1944).

by swarms of wasps. Additional data are required on the annual abundance of wasps ranging over continental areas and in insular regions (*e.g.* the British Isles), and their correlation with the climatic conditions prevailing in both areas.

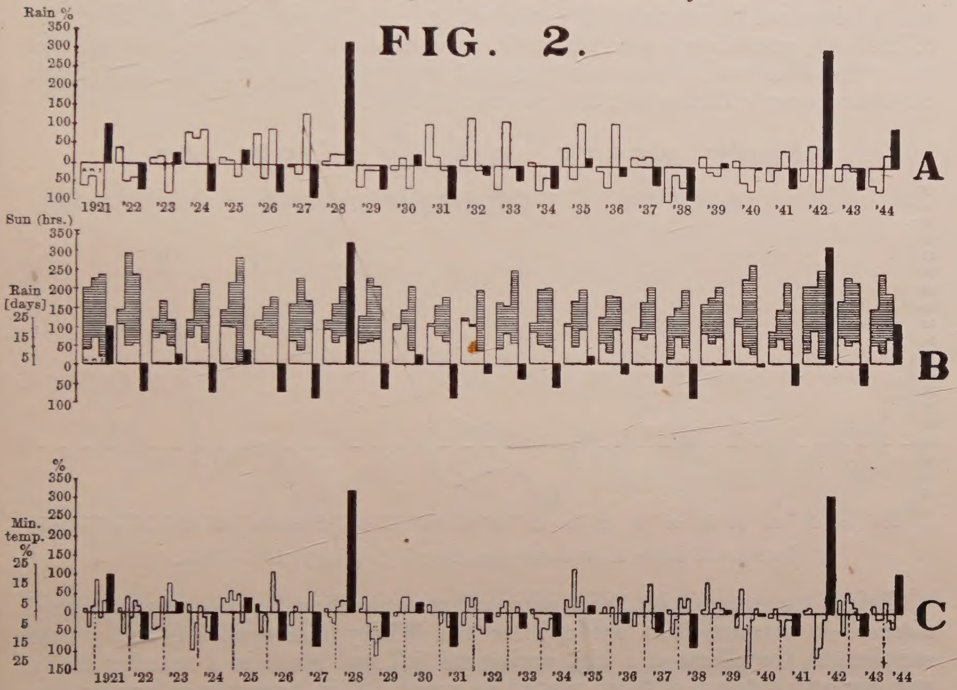
The fact that Beirne's theory did not hold good for some years resulted in consideration being given to other factors, namely, the effect of (1) spring rainfall; (2) spring temperatures; (3) autumn temperatures; (4) winter temperatures; (5) humidity; (6) availability of food for the foraging females in spring; and (7) natural enemies.

Species of Wasps Concerned.

The species of *Vespula* concerned in the Wisley observations were the ground-building *V. germanica* F., *V. vulgaris* L. and *V. rufa* L., and the aerialnest building *V. sylvestris* Scop. and *V. norvegica* F. Of these five species, *V. vulgaris* and *V. germanica* were the commonest, though the ratio between them varied from one season to another. *V. rufa* was fairly abundant in most years; the number of nests of *V. sylvestris* in any one year varied from one to five; while the least common species was *V. norvegica*.

Beirne (*loc. cit.*) states that " the five species vary in abundance in relation to each other in each season, but it would seem that in years of abundance more than one species is commoner than usual." This observation is confirmed by the Wisley observations, and one concludes that several if not all the species are affected by certain controlling factors in the same way.

FIG. 2.



Approximate Degree of Wasp Abundance and Scarcity correlated with :—(A) Mean Rainfalls of April, May and June; (B) Sunshine (in hours) and Rainfall (in days) of April, May and June; and (C) Temperature Minima of October to March.

(1) The Effect of Spring Rainfall.

Beirne concluded that in seasons of wasp abundance the rainfall during April, May and June was low and in seasons of scarcity it was high (fig. 2, A) and, further, that seasons of abundance and scarcity usually occur in pairs (fig. 3).

The presentation of the Wisley data follows that of Beirne where the height of each black block represents the approximate degree of wasp abundance, the average being represented by the horizontal line (fig. 2). The three open blocks represent the mean monthly rainfalls for April–June in each year as compared with the average for the three months (1921–44) shown again by the horizontal line. The meteorological data throughout are those recorded at Wisley at the same place as the records for wasp abundance.

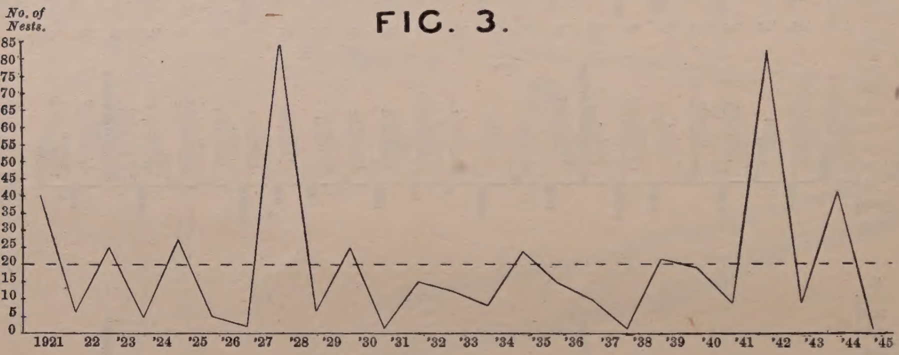
The figures are in general agreement with those obtained by Beirne, namely, that spring rainfall is an important factor in regulating abundance, at least, in 16 out of the 24 seasons covered by them.

Walsh (1945) is somewhat critical of the statement that the determining cause of wasp abundance in any given year is low rainfall during the spring months of the year, but his data refer only to one year (1944) and to two localities (Llandudno and Scarborough). While the figures obtained at Llandudno lend good support to Beirne's theory, those from Scarborough do not.

Scott (1945) bases his remarks upon the meteorological data of the Henley district, and states that the winter season 1942–43, preceding a summer when wasps were very scarce, shows several very wet months—October, December and an exceptionally wet January; while, though March and April, 1943, were much drier than the average, May was wetter. On the other hand, in the winter of 1943–44, preceding a summer with an abundance of wasps, all the months except October were below the average and some very much so, while the rainfall continued scanty throughout the summer of 1944.

WASPS' NESTS WISLEY. 1921–45.

FIG. 3.



Seasons of Wasp Abundance and Scarcity, Wisley, 1921–1945.

Beirne suggests (*in litt.*) that some other controlling factor—an unspecified disease—is concerned to account for the Wisley discrepancies, and would supplement the effects of a high spring rainfall and result in a scarcity in the summer and autumn of those particular years. This, however, is largely conjecture owing to the absence of data upon the incidence of disease among wasps in different years. In accepting the suggestion that a " natural enemy " is concerned, it may be argued that some such limiting factor became scarce after the two seasons of wasp scarcity (1926–27), thus allowing the wasps to increase unchecked in 1928 despite the unfavourable spring as regards rainfall (fig. 2, A); and, again, that this same limiting factor again increased during the years 1931–34, becoming most abundant in 1934 in spite of a favourable spring. Continuing this line of reasoning, the great scarcity of wasps in 1934 produced a corresponding scarcity of the " natural enemy " in 1935, thus allowing the wasps to increase unchecked in that year. The same limiting factor may have been concerned during the years 1935–37, causing a scarcity of wasps in 1938, despite a very favourable spring so far as rainfall was concerned.

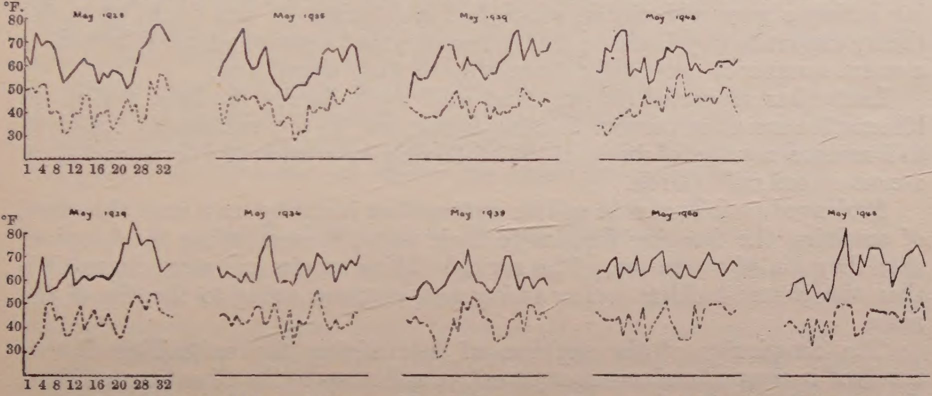
Wasps were very abundant in 1928 despite the spring rainfall being above the average, and this was followed by a year of scarcity in spite of low rainfall. Similarly, these remarks apply to some extent to the years 1921 and 1922, and to 1942 and 1943.

An important feature that is not demonstrated by monthly rainfall figures is the intensity of the rain that falls, and information is required as to whether prolonged periods of dull weather and of light continuous rain are more detrimental to wasps than a month with the same amount of rain falling over a brief period of a few days. An attempt has been made to indicate the intensity of rain (fig. 2, B) by plotting the fall in inches together with the amount of sunshine in hours for the months April–June. A month with a total low rainfall may have a short but very wet period, and this may prove as important a controlling factor upon wasp abundance as a month with a far higher rainfall spread over many days.

An indirect effect of heavy rain during the spring months may be the flooding-out of nesting-sites owing to the raising of the water-table. This effect was observed at Wisley in June, 1944, when three nests of *V. vulgaris* were flooded out following heavy rains (2·14 inches in 13 days), which raised the water-table in a low-lying part of the Gardens.

FIG. 4.

MAXIMUM AND MINIMUM TEMPERATURES .



The Effect of May maxima and minima upon Wasp Populations (see text).

(2) The Effect of Spring Temperatures.

Untimely activity in spring due to a period of high temperatures followed immediately by a period of colder weather and renewed torpor is liable to prove fatal to many hibernating insects. High mortality among insects may follow a succession of unusually low night temperatures and rapid fluctuations of temperature during the phase immediately prior to their renewed activity. The effect of such fluctuating temperatures on the duration of life in social wasps is a problem requiring fundamental research, for the observations that have been made are casual and have not been followed up with critical data.

Insects become restless during the later phases of hibernation when high maximum temperatures occur in late winter and early spring. Such premature awakening may result in exhaustion owing to the sudden demand upon the diminishing stores of fat. Female wasps are occasionally observed to fly in February and March when high day temperatures are recorded, and some have been observed to fall exhausted owing to their inability to replenish their stores of internal fat.

The "critical point" or "undercooling" where freezing begins in insects varies with the species and, while most will survive a single, few can withstand a double undercooling—a fact observed in the case of the larvae of the Gooseberry Sawfly, *Pteronidea ribesii* Scopoli (Fox-Wilson 1939).

During the period when insects are being restored to normal temperatures in early spring following hibernation their revival is normally certain, but for them to be subjected to rapid fluctuations and to more than one undercooling may prove fatal. The tendency for frosts to occur in late spring (mid-May) following a spell of warm weather is frequent in many districts. This applies to Wisley in particular, and such conditions have been observed to affect the insect newly emerged from its hibernaculum. The mortality figure among the recently revived insects is higher when there are rapid fluctuations in temperature than when fairly constant temperatures prevail. A hibernating insect subjected to such fluctuations so that it undergoes periods of rewarming and recooling is thrown back upon its metabolic reserves and is then more liable to fall a victim to disease. The fact is established that a persistently cold winter favours hibernation among insects, and that in such seasons there is a lower mortality among them than in what may be termed " unseasonable weather " (Uvarov 1931).

The hibernating insect may even undergo periods of rewarming and recooling during a very cold winter, which fact is sufficient to cast doubt upon the theory expounded by Leclercq (1944), namely, that a severe winter followed by a warm summer is necessarily favourable to wasp abundance.

Latter has suggested (*in litt.*) that mild spells during the later periods of hibernation are an important limiting factor, and he was sufficiently confident to forecast a scarcity of wasps in 1945 following a record mild February and an almost record mild March.

Prolonged periods of cold and/or wet weather in spring may have the effect of confining the foraging females to their nests, thus affecting the brood so that they die of starvation. The aerial-building species are more susceptible than the ground-builders to low spring temperatures owing to the site of the nests.

The complexity of the problem of determining the controlling factors involved in wasp abundance is apparent on reference to the climatic conditions that prevailed during the springs of 1935, 1938 and 1943. The nest population figures for 1935 were 20 per cent. above the 24-year average, and this despite the high rainfall of April and June (fig. 2, A). Neither the rainfall during these months, nor the severe spring frosts experienced in mid-May (fig. 4), nor the consistently high temperatures that prevailed during the previous autumn and winter (fig. 2, C) proved to limit wasp abundance.

Again, there was a marked scarcity of wasps in 1938 despite two factors, namely, (i) the great scarcities of wasps in the two previous years, and (ii) the low spring rainfall. In this season, however, there occurred in May a period when the temperature fluctuated markedly (fig. 4), and this factor may have proved to be the limiting one. Similarly, in 1943, the severe frosts that occurred in May could be considered as a controlling factor in wasp abundance.

Spring frosts occur frequently when the day temperatures are high, and maxima of 70° F. to 80° F. are reached when the minima are ± 30° F. (fig. 4—1929, 1934, 1939, 1943 and 1945).

Not only high, but average day temperatures, accompanied by periods of intense sunlight in late winter and early spring may affect the hibernating females so that they become prematurely aroused from their torpor when such untimely activity may prove fatal. The effect of sunlight during these seasons is discussed later (*see* Section 4).

A combination of factors is undoubtedly concerned on occasions in affecting wasp abundance, for instance, the scarcity of wasps in 1941 may have been due to the combined effects of severe frosts in May and to the high June rainfall of that year. On the other hand, a similar combination of factors in 1944 did not have the same limiting effect upon the population.

(3) The Effect of Autumn Temperatures.

The effect of autumn temperatures upon female wasps about to undergo their diapause may affect the degree to which the hibernating insects may withstand winter cold. The process of " hardening-off " is dependent upon the temperature gradient during the pre-hibernation period. A mild and damp October followed by a spell of severe frosts would prove more fatal than a dry autumn with gradually decreasing temperatures which would not hinder the natural processes.

The temperatures prevailing in October (fig. 2, C) may have some effect upon abundance the following year. In the nine years of abundance, the temperature during the previous October was *above* the average in 7 (78 per cent.) and *below* in 2 (22 per cent.), but in the 15 years of scarcity the number of warm Octobers was not less than the number of cold, namely, 8 (52 per cent.) being *above*, and 6 (40 per cent.) being *below* the average.

The gradual hardening process that occurs during the onset of complete dormancy of hibernating insects is a natural phenomenon, but it is known that a number of insect species are unable to survive even a single undercooling at this period, though some can survive the freezing of their tissue fluids.

(4) The Effect of Winter Temperatures.

Consideration may first be directed to the theory expounded by Leclercq (1944) that a severe winter followed by a favourable spring and a warm or hot summer appear to provide conditions favourable to the multiplication of wasps.

The following years—1924, 1934, 1938, 1940, 1941 and 1942—were what may be termed years in which the preceding winter was cold or very cold and the summer warm or hot—this applying specially to 1941. The nest population at Wisley was above the average in one only (1942) of the six years under review. There was no general indication that a severe winter preceding a pleasant spring and a hot summer provide optimum conditions for wasp abundance. In view of the longer series of observations obtained at Wisley, Leclercq's statement based upon two years' observations (1942 and 1943) is not acceptable.

There is some indication that a warm winter favours abundance in the following summer, but that cold winters do not produce a scarcity to the same degree.

In the nine years of abundance, the temperature was *above* the average in 32 (59 per cent.) of the 54 winter months, and *below* the average in 15 (26 per cent.). In the fifteen years of scarcity, the effects of the preceding winters are less marked, as 41 (46 per cent.) of the 80 winter months were *below* and 37 (41 per cent.) were *above* the average (fig. 2, C).

The three cold and dry winters (1923–24, 1928–29, 1930–31) were followed by scarcities; three of the five warm and wet winters (1922–23, 1927–28, 1929–30) were followed by an abundance, but two (1921–22, 1936–37) were followed by scarcities. Again, a warm winter with an average rainfall (1925–26) was followed by a scarcity.

The physiological processes concerned with the hibernation of insects, together with the effects of low temperatures on winter mortality, have been fully discussed elsewhere (Uvarov 1931), and no further reference need here be made to them. However, the direct and indirect effect of the microclimatic conditions prevailing in the hibernacula of wasps have not received the attention they deserve.

Marked fluctuations in air movement, temperature and humidity undoubtedly occur in lofts, sheds (favoured by *V. vulgaris*), attics, thatched roofs, hay-ricks, under the bark of trees (favoured site for *V. germanica*), and other shelters chosen by the hibernating female wasps, but scientific data upon such are not available.

The factor of humidity is important in that it influences the body temperature of the insect through its effect on evaporation and that, except under low temperatures, the body is invariably warmer in moist than in dry air and is cooler in moving than in static air.

The female wasp during its diapause is subjected to special atmospheric conditions wherein high atmospheric humidity would tend to influence the degree of susceptibility of the organism to fluctuating temperatures and, it is reasonable to suppose, to the development of entomogenous fungi. The opinion of Dr. T. Petch was sought in this connection, but he was unable to confirm the fact that hibernating wasps are affected to any degree by fungal organisms, adding that he had found only two dead wasps attacked by the commonest entomogenous species of fungi during the past ten years and had never found any species peculiar to wasps. Nevertheless, the possibility that mortality occurs among the hibernating " queens " through the agency of such disease organisms should not be overlooked.

A further factor affecting the hibernating female wasp that deserves attention is that of the intensity of light penetrating into the hibernaculum. The following observations were kindly supplied by Mr. Latter (*in litt.*), who has kept a female wasp under close observation during the past few months, and noted its reaction to temperature and to light. A mild spell of weather that occurred in December, 1945, brought the maxima to 52·0° F. and with minima of 45° F. over a period of five days, but the wasp showed no sign of being aroused until the morning of the 19th, which was very bright and sunny following a period of dull, sunless days. On this date, she brought her wings up over the dorsal surface for a few hours, then relapsed into the normal posture during the afternoon, and did not move her position. A further mild spell occurred from 9th to 12th January, 1946, with mean maxima of 53° F. and minima of 46° F. The first three days were dull and sunless, and the wasp showed no sign of being aroused, but the 12th was brilliantly fine, which resulted in the wasp moving about 2 inches across the box towards the narrow slit through which light enters the hibernaculum. The insect again settled down into the correct hibernation attitude. On the 27th January, however, although the maxima for the previous two days had not reached 44° F., and the room in which the insect was situated recorded a temperature of 49° F., the sun was shining brightly after the fog had cleared at 11.0 a.m., which aroused the insect so that it walked about in the box for some time. The actinic value of sunlight was decidedly greater than it was in December, and light would appear to have been the factor concerned with the awakening of the dormant insect to considerable activity, and more especially when the maxima were lower than those recorded on the first two occasions. Thus, Latter suggests that light may have a profound effect upon the hibernating insect.

It is a matter for investigation to correlate winter temperatures with sunlight to ascertain whether an abundance of wasps follows a period of mild spells accompanied by consistently dull weather during the preceding winter; and that a scarcity exists when mild spells in the preceding winter are accompanied by a number of bright sunny days.

(5) The Effect of Humidity.

Atmospheric humidity is an important factor, associated as it is with temperature, and one that may have both a direct and indirect effect upon the hibernating females. The indirect effect would be that high humidity might predispose the insect to disease, but data are not available to substantiate this suggestion.

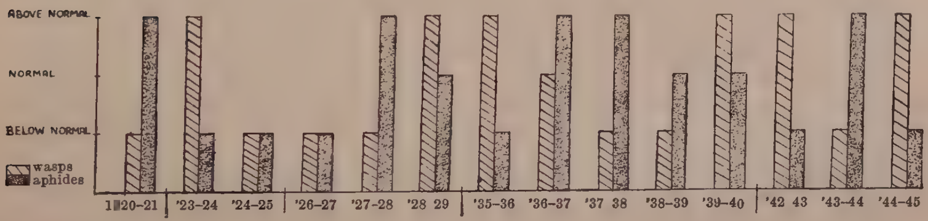
The period of hibernation is stated to become extended in the absence of moisture, while the percentage of mortality is higher (Uvarov 1931). The moisture factor is suggested as being directly concerned with affecting the water balance of the hibernating insect, and may be an even more important one than temperature both in the inception of dormancy and in its normal end. Problems associated with hibernation and with diapauses are far from being solved despite their great biological significance.

(6) The Effect of Available Food.

The movements of the females newly emerged from their hibernacula are attended by great activity in their search for food for their brood. Female wasps are seen actively foraging for food along hedgerows and elsewhere during the early days of spring, and collect Aphides, small caterpillars (partiality being given to the larvae of the Gooseberry Sawfly, *Pteronidea ribesii* Scopoli), Leaf-Hoppers, Cercopids and small flies; nectar from fruit blossom, especially Gooseberry (Fox-Wilson 1933) and ornamental shrubs, e.g. *Cotoneaster horizontalis* and *Symphoricarpus racemosus*; honeydew excreted by homopterous insects (Aphides and Coccids); and the sticky exudations from *Cistus* and other buds. The factor of phenological adjustment between the foraging queens and the availability of food is important, and should be considered so far as it affects the normal rate of development of the new colony.

FIG. 5.

RELATIONS BETWEEN VESPIDS AND APHIDES (APHIS FABAE SCOP.).



In this connection, it has been suggested that some relationship exists between the incidence of Vespids and Aphides—the theory being that an abundance of wasps in one year may lead to a scarcity of Aphides the following year, and vice versa. I am again indebted to Mr. Latter for sending me data relative to the incidence of wasps and of the Bean-Spindle Aphid, *Aphis fabae* Scopoli, upon which the accompanying chart (fig. 5) has been prepared.

Some correlation would appear to exist between the incidence of these two insect groups in 10 out of the 14 years recorded. The unsatisfactory feature of the data, however, is that they refer not only to different districts (Wisley and the Eastern Counties), but to one species only of Aphides. It is necessary to obtain a long series of both Vespid and Aphid populations from the same district in order to prove whether there exists any inter-relationship between them.

The difference in wasp populations between places not far apart is often considerable, this being confirmed by reading the correspondence columns of the daily and horticultural press during years of marked scarcities and abundance of Vespids.

(7) The Effect of Natural Enemies.

Apart from a number of " guests " (*e.g.* certain species of beetles, flies and moths and/or their larvae; of woodlice; and of mites) that inhabit wasp nests and act as scavengers, little information is available on the effect of primary parasites as limiting factors in abundance. An important primary parasite is *Rhipiphorus* (*Metoecus*) *paradoxus* L., but data upon the mortality of social wasps due to this species are lacking.

Predatory enemies include web-spinning spiders, which feed upon both " workers " and " queens," the latter being frequently captured in autumn when seeking their hibernacula in sheds, lofts and outhouses and, again, in spring as they leave their overwintering quarters. The badger is predatory upon Vespids, seeking out their nests and devouring the brood of ground-building species in summer and early autumn. A percentage of wasp nests is annually destroyed at Wisley by these animals, " setts " of which are found in a hillside within the area of the Gardens.

The rôle of entomogenous fungi as a possible limiting factor in wasp abundance has been discussed elsewhere (see Section 4).

The endoparasitic *Gordius* worms take their toll of wasps, and observations made by Latter and myself indicate that these parasites are controlling factors affecting chiefly the drones. In this connection, Latter refers to the " Wasp Year " of 1893 when he found that every male—several score of them—in one large nest was affected by these worms. One effect upon the host is to produce castration, resulting in loss of fertility. Whether, he adds, this was the factor concerned, the result was that the following year (1894) was one of wasp scarcity.

Beirne suggests that another limiting factor is disease (unspecified) that may account for a high mortality among the larvae. He concludes that in seasons of wasp abundance disease is correspondingly increased but, owing to its increase being at a slower rate than that of the wasps, the effect is not immediate.

The persistent slaughtering of the " queens " in spring by gardeners and fruit-growers may account for a considerable percentage of females, but the effect of the above-mentioned parasites and predators as well as of human agencies upon wasp population is negligible compared with the mortality arising from the effect of unfavourable weather conditions at certain phases of their life cycle.

ACKNOWLEDGEMENTS.

I desire to express my very sincere thanks and acknowledgements to Dr. B. P. Beirne for his assistance in interpreting the results obtained at Wisley and for many helpful suggestions on the problems relating to wasp abundance; to Mr. O. H. Latter, M.A., for allowing me access to all his data and observations and for giving full permission to make use of them; to my colleague, Mr. W. D. Cartwright, for providing the local meteorological records; and to my wife, and to my Assistant, Miss J. Maynard, for preparing the several charts illustrating this paper.

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Book Notice.

Butterflies and moths in Britain. By V. Temple. 8vo. London (B. T. Batsford, Ltd.) (1946). Pp. viii + 120, 10 coloured plates, 56 black plates, 57 text figs. Price 12*s*. 6*d*.

This book may truly be described as " by " Miss Temple, for not only the text but the colour drawings and the line sketches are all her work.

The opening sentences of the book give a good indication of the intimate style adopted : " A young friend of mine (aged 7) said to me the other day : ' I've found a butterfly for you. It's not very big, so I think it must be a young one. I squashed it, in case it might eat my clothes.' And he produced, from a matchbox, the battered remains of a Yellow Underwing Moth."

The outstanding feature of the book is the illustrations. The coloured plates are reproduced by lithography and make most attractive pictures, and the many photographs cover not only the perfect insect, but include many figures of eggs and larvae.

As will be noted from the title, the book does not claim to include all the British Lepidoptera, and a systematic arrangement has not been adopted.

As the author says in her preface, she has described the butterflies and moths she knows, and written of the countryside that is their setting.

ON THE MALPIGHIAN TUBULES OF *FORFICULA AURICULARIA* (DERMAPTERA)

By H. Henson, B.Sc., Ph.D., F.R.E.S.

(*Lecturer in Zoology, University of Leeds.*)

Introduction.

In recent years it has become increasingly evident that the study of insect metamorphosis must be integrated with that of embryology if significant progress is to be made. From this viewpoint the growth and development of Malpighian tubules has proved to be of considerable value. Their suitability for study is further enhanced by the comparative simplicity of certain aspects of their tissue growth and differentiation.

The problem has already been approached in a study of *Blatta orientalis* (Henson 1944), but the large number of tubules, and the fact that the various instars are not easily distinguished from one another, made it impossible to attain the desired precision. These difficulties do not exist in the case of *Forficula*, which is therefore much more favourable material for an investigation of this particular problem.

It also happens that *Forficula* was the actual genus in the embryonic development of which Heymons (1895) claimed to have shown an ectodermal origin for the mid-gut. This claim has had an unfortunate and depressing influence upon the proper understanding of the fundamental processes of insect embryogenesis and any enquiry which extends our knowledge of the true morphology of the insect gut is of real value and theoretical importance.

My best thanks are accorded to Professor E. A. Spaul for kindly criticism and advice.

II. Material and Methods.

No difficulty was experienced in obtaining all stages of the life history from eggs to adults, and no undue difficulty was encountered in rearing specimens in glass vessels in the laboratory. There was, however, a suggestion that growth was slower in the laboratory than in the field and it is probable that the addition of pollen to the diet of carrots, lettuce and dead flies would have been beneficial.

Close observation of members of the same brood showed quite definitely that there are five instars, easily distinguished from one another by the number of antennal joints. The first instar has 8, the second 10, the third 11, the fourth 12, and the adult 14.

Dissections were carried out in 1% salt solution or in 30% alcohol. For microscope preparations specimens were fixed in Carnoy, double embedded in celloidin and wax, and stained with iron haematoxylin and Orange G. Delafield's hæmatoxylin was used for whole mounts.

III. ANATOMY OF THE TUBULES.

As in most insects, the Malpighian tubules of *Forficula* are slender filaments attached to the alimentary canal in the neighbourhood of the junction of the mid-gut and hind-gut. They are attached to the gut in four groups, each group containing five tubules. Bordas (1898) is incorrect in describing a total of 8–10, or about 12, arranged in two groups. In a few specimens one of the four groups may contain six tubules instead of five but this variation is not very frequent. At the point of attachment to the gut the base of each tubule group is swollen to form a basal vesicle. In *Blatta* a similar swelling is formed by the confluence of the bases of the tubules but it is not a definite differentiated structure as in *Forficula*.

Owing to the twisting of the gut the positions of attachment of the four groups can only be inferred from their relations to the lines of attachment of the transverse muscles of the hind-gut. Careful examination suggests that they are dorso-lateral and ventro-lateral in position (figs. 1, A and 1, B).

The newly hatched nymph has only four tubules, two dorso-lateral and two ventro-lateral, which, since they arise during embryonic stages, are known as primaries. After hatching a single new tubule appears on the posterior side of each primary, the four new tubules thus formed constituting the first instar secondaries. Similarly a new secondary tubule is added to each group in each of the second, third, and fourth instars, always on the posterior side. The result of this mode of growth is that the five tubules are arranged in a longitudinal row along the gut, the oldest being the most anterior and the youngest the most posterior (fig. 1, A).

In *Blatta* the newly hatched nymph has only the dorso-lateral and ventro-lateral tubules as in *Forficula*, but during the first instar another pair appears in the lateral position. These undoubtedly belong to the series of first instar secondaries and their presence indicates that the corresponding primaries have been suppressed. In *Forficula* therefore it seems that all the lateral tubules have been suppressed, secondaries as well as primaries.

In the newly hatched nymph the primary tubules occupy definite and constant positions in the body cavity (fig. 1, B). Here, unlike *Blatta*, none of the four tubules is in any way associated with the rectum, all pass forwards along the mid-gut. In the first instar two of the secondary tubules are found to pass into the posterior parts of the body cavity but no definite association with the rectum has been observed. In the later instars no precise arrangement of the tubules can be recognised.

In the adult female the larger tubules, when alive, are about 16 mm. in length and 0·10 mm. in diameter, although the latter dimension varies considerably. As in *Blatta*, the tubule is divisible into two regions, a short upper segment 0·30–0·65 mm. in length, and a long lower segment comprising the remainder of the tubule. The upper segment is always clear and transparent and never contains excretory material even when the lower segment is full of concretions (fig. 1, C). Hence it seems probable that the mechanism of excretion associated with the development of upper and lower tubule regions in *Rhodnius* (Wigglesworth 1931) is also present here, although it is not unlikely that there are differences of detail associated with the extreme shortness of the upper segment. In so far as simple observational evidence is adequate the same mechanism has thus been indicated in *Blatta* (Henson 1944), some Ephemeroptera (Henson 1946a) and in *Forficula*.

The cellular construction of the tubules is quite different from that of *Blatta*

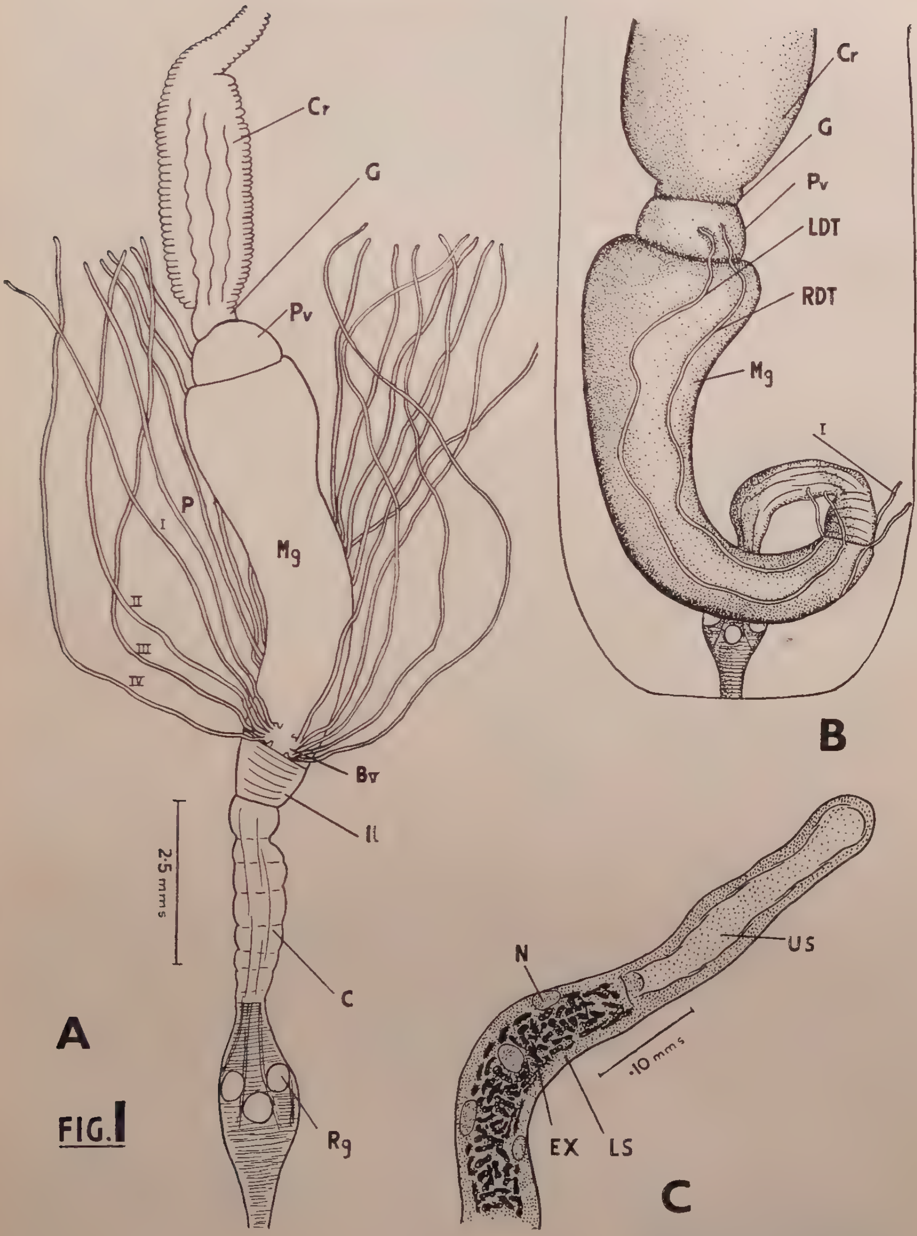

Fig. 1.—A, alimentary canal of the adult; B, the same in a first instar (in situ); C, the upper end of a tubule in a second instar (from life). Bv = basal vesicle, C = colon, Cr = crop, Ex = excretory matter, G = gizzard, Il = ileum, LDT = left dorsal tubule, LS = lower segment, Mg = mid-gut, N = nucleus, P = primary tubule, Pv = proventriculus, RDT = right dorsal tubule, RG = rectal gland, US = upper segment, I, II, III, IV = first, second, third and fourth instar secondary tubules. (In view of discrepancy with other published figures it may be noted that the gizzard, although small, is quite distinct from the proventriculus.)

and more nearly resembles that of the Lepidoptera. As in the latter group, each tubule is composed of only two rows of cells (figs. 3 and 4). (That some of the figures do not show two rows of cells is due to the specimens having become twisted on the slide in the course of preparation.) The individual cells show a typical striated border on the side towards the lumen.

The mode of attachment of the tubules to the gut is seen in fig. 2, A. The basal vesicle, composed of squamous epithelial cells, opens into the alimentary canal at the junction of the mid-gut and hind-gut. Its actual opening is protected by a double fold of tissue which has every appearance of being a valve mechanism, preventing regurgitation from the gut into the cavity of the vesicle. This fold, however, is not present in the youngest stages, a fact which renders its interpretation as a valve somewhat less definite.

IV. Development of the Tubules.

In the newly hatched nymph there are, as already mentioned, only the four primary tubules. A few days later the first instar secondaries appear as tiny buds on the posterior side of each primary. In longitudinal section (fig. 2, B) it is seen that the basal vesicle is already clearly differentiated and that the young tubule is originating from an embryonic zone on its posterior side. Mitotic division of the cells of this region causes a protuberance which gradually extends outwards to form the young tubule. Further elongation is effected by continued cell division along the whole length of the tubule—there is no localised growing region. From the beginning a lumen is present and probably in communication with the cavity of the basal vesicle. A mass of embryonic mesenchymatous tissue surrounds the young tubule and ultimately produces a trachea and a thin investing connective tissue sheath.

In specimens hatched in the laboratory the first instar lasted about 24 days. The secondary tubules first became visible on the 5th day—an indication that their formation began about the time of hatching. By the 21st day they had acquired only about one-third of their ultimate length but by the 24th day, when ecdysis occurred, they had attained their full length. There are thus two quite different growth periods, a long slow phase, followed by a very short rapid phase. In the first phase transverse sections of the young tubule show approximately five rows of cells (fig. 3, C—the section is two cells thick and hence shows ten nuclei). In the second phase transverse sections may show any number of cells from five to two (fig. 3, D). Thus the slow elongation of the first phase is brought about by cell division, the rapid elongation of the second phase by the shifting of the cells on one another until only two rows are present. Differentiation is completed at the period of the ecdysis by the enlargement of the cells and the expansion of the lumen.

The same process occurs in all the subsequent nymphal instars. Within a few days of each ecdysis a young secondary tubule becomes visible and passes through the three phases of "cell multiplication," "cell re-arrangement," and "cell differentiation."

In about 100 specimens examined five adults had six instead of five tubules in one of the groups, two fourth instars had a group of five instead of four, two third instars had a group of four instead of three. In all these cases the additional tubule was not in antero-posterior alignment with the rest but seemed

Fig. 2.—A, longitudinal section through tubule attachment in a fourth instar; B, the same in a first instar. Bv = basal vesicle, Df = "valvular" fold (absent in B), Hg = hind-gut, Mg = mid-gut, P = primary tubule, I, II, III, IV as in fig. 1.

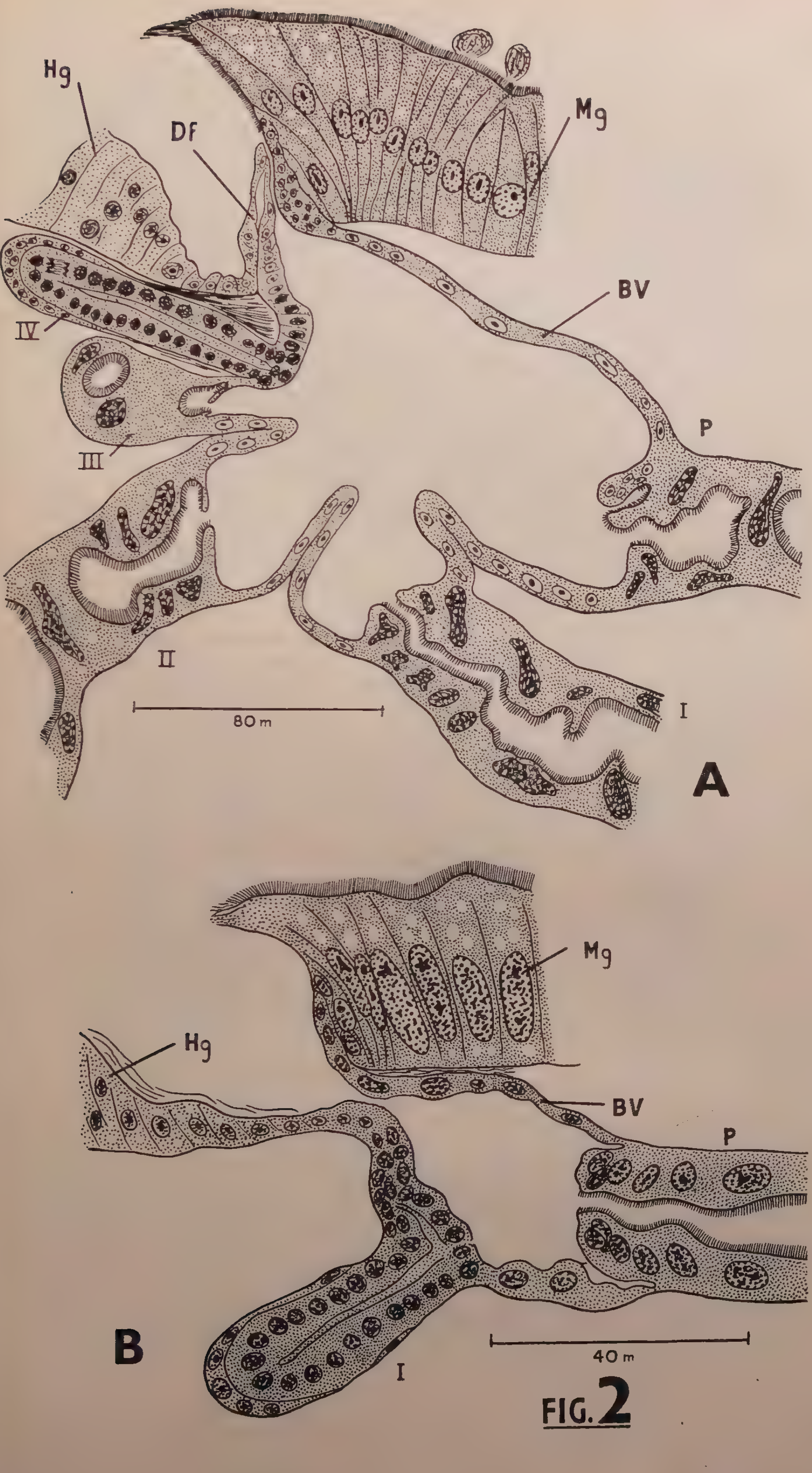

FIG. 2

to branch out from the base of one of the others. It thus seems likely that it arose by the division of an originally single rudiment. It is of interest to note that in *Machilis* (Oudemans 1888) all the tubules are of this same double type.

One of the great advantages of *Forficula* for the present study is that individual tubules can be followed throughout the life history. The primary tubules are, of course, already present at the time of hatching. Even thus early they are fully differentiated and possess the normal form with two rows of cells (fig. 3, A and B). The nuclei are roughly spherical and about 10 μ in diameter. No appreciable change of form occurs in the first and second instars (fig. 3, B and E), but soon after the second ecdysis the nuclei are seen to have become slightly oval and approximately 20 μ in diameter (fig. 3, G). The tubule itself increases appreciably in diameter in the third, fourth and fifth instars but no further significant alteration in nuclear size has been observed (*v.* Table 1).

The first instar secondary tubule in its "multiplication" stage (fig. 3, C) has nuclei 5–6 μ in diameter. No change occurs during the "cell re-arrangement" phase but in the differentiation stage at the first ecdysis the nuclei enlarge slightly and become 7–8 μ in diameter (fig. 3, F). At the second ecdysis the nuclei double their previous diameter, becoming 15–16 μ (fig. 3, H), just as in the case of the primaries at the same stage. In the fourth and fifth instars the tubule again expands but the nuclei do not show any further appreciable alteration.

The second instar secondaries are like their predecessors in the first instar. In early stages the nuclei are 5–7 μ in diameter, and remain so until the time of the second ecdysis when, as in the previous instances, they are doubled and become about 14 μ in diameter (fig. 3, J).

The third instar secondaries behave in much the same way. The nuclei are small to begin with but double in size at the ecdysis which occurs at the end of the instar. Similarly with the fourth instar secondaries in which the nuclei undergo marked enlargement at the fourth ecdysis (fig. 4, A and B). It should be noted that at the third and fourth ecdyses none of the other tubules shows any marked change in nuclear diameter (Table 1).

TABLE 1.

Diameter of tubule nuclei—in μ.

	Primary	I	II	III	IV
1st instar	10	5–6	—	—	—
2nd „	10	7	5–7	—	—
3rd „	20	15	14	6–7	—
4th „	17	15	15	15	6–7
Adult	19	16	13	15	14

It may be noted that there is no doubling of nuclear diameter at the first ecdysis, that all the tubules suffer this change at the second ecdysis, and that at the third and fourth ecdysis the change is restricted to the tubules newly formed in the preceding instar. No significance can be attached to the smaller variations although it is possible that the secondaries do tend to have somewhat smaller nuclei than the primaries. All the nuclei of the tubules do not become enlarged, a few remain comparatively small (fig. 4, A, 4, B).

According to Berger (1938), the enlargement of the nuclei in the hind-gut

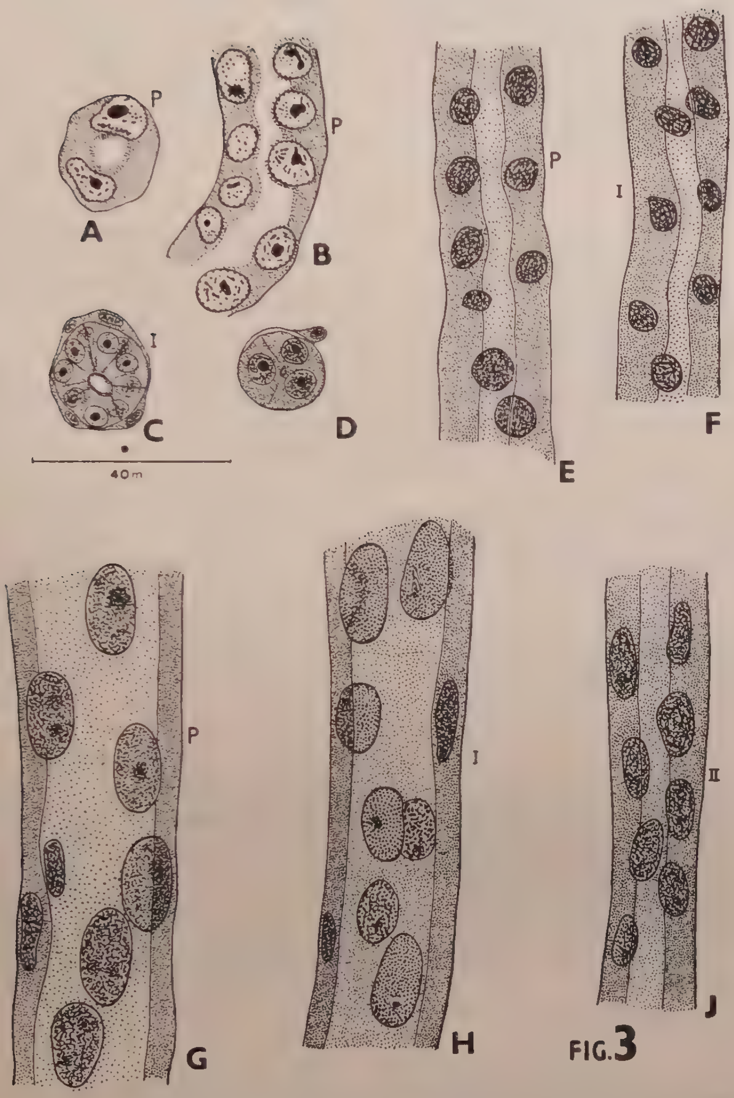

FIG. 3

Fig. 3.—A, B, C, D, tubules of the first instar; A, primary tubule in transverse section; B, the same in longitudinal section; C, the first instar secondary in "cell multiplication" stage; D, the same in "cell rearrangement" stage. E, F, second instar tubules in surface view; G, H, J, third instar tubules in surface view. All to same scale. P, I, II = primary and first and second instar secondary tubules.

of the larva of *Culex* is due to increasing degrees of polyploidy, chromosome numbers being doubled as many as four times. If a similar explanation can be applied to the Malpighian tubules of *Forficula* it would seem that almost all the nuclei are polyploid and that a large increment of the increase is due to changes occurring at ecdysis, particularly the second ecdysis. However, the problem is essentially cytological and the present results do not permit any far-reaching conclusions.

V. DISCUSSION.

In connection with the general theory of insect metamorphosis, it has been suggested that insect growth is cyclical, each instar being the product of a growth process similar in essentials to embryonic development (Henson 1946b). These developmental cycles respond to hormonal control (Wigglesworth 1940) and are subject, in larval stages, to some degree of suppression which prevents the full realisation of their potentialities.

In the case of the Malpighian tubules there is in each instar a developmental cycle which results in the formation of a young secondary tubule. As in *Blatta*, this arises at the level of the inner end of the " proctodaeum," probably much as in the embryo. Mitotic division of the cells of the young tubule continues throughout most of the period of the instar but final differentiation is complete at about the time of the next ecdysis.

The simplest mode of growth of Malpighian tubules yet described is found in *Blatta* (Henson 1944). The young tubule arises by mitotic division of embryonic cells and elongates as division proceeds because the resulting cells remain in five longitudinal rows. Whether this is achieved by persistent cell shifting or the restriction of cell division to the one longitudinal direction is not clear. Final differentiation involves no more than a comparatively slight enlargement of the constituent cells. In *Forficula* the same control of cell division also produces a young tubule with five rows of cells but mitosis ceases *before* differentiation occurs and extensive changes in cell arrangement produce a tubule with only two rows of cells. In *Pieris brassicae* (Henson 1937) there are no secondary tubules but the embryonic development of the primaries shows the same essential features as the development of the secondaries in *Forficula*. Cell division is restricted to the first half of embryonic life, in the second half elongation is brought about by cell rearrangement which reduces the number of rows from about fifteen to two. Thereafter, in larval life, considerable nuclear enlargement takes place, comparable with that which occurs in the young stages of *Forficula*.

In these three types *Forficula* clearly occupies a middle position. In some respects it is much more akin to the Lepidoptera than to the Orthoptera from which one may perhaps infer that the " suppression influence " is greater in *Forficula* than in *Blatta*, and hence that the Dermaptera are closer to the holometabolous groups than are the Orthoptera.

The changes in the size of the nuclei in the cells of the Malpighian tubules during the life history have an important significance, as yet undetermined, for the problem of growth. At the moment it seems safe only to conclude that the developmental cycles of the nymphal instars have different intensities—for example no doubling of nuclear diameters occurs at the first ecdysis, doubling occurs in all the tubules at the second ecdysis, and only in the youngest tubule at the third and fourth ecdyses.

The morphology of the Malpighian tubules of *Blatta* (Henson 1944) suggest that the primitive insect arrangement was six primary tubules with numerous

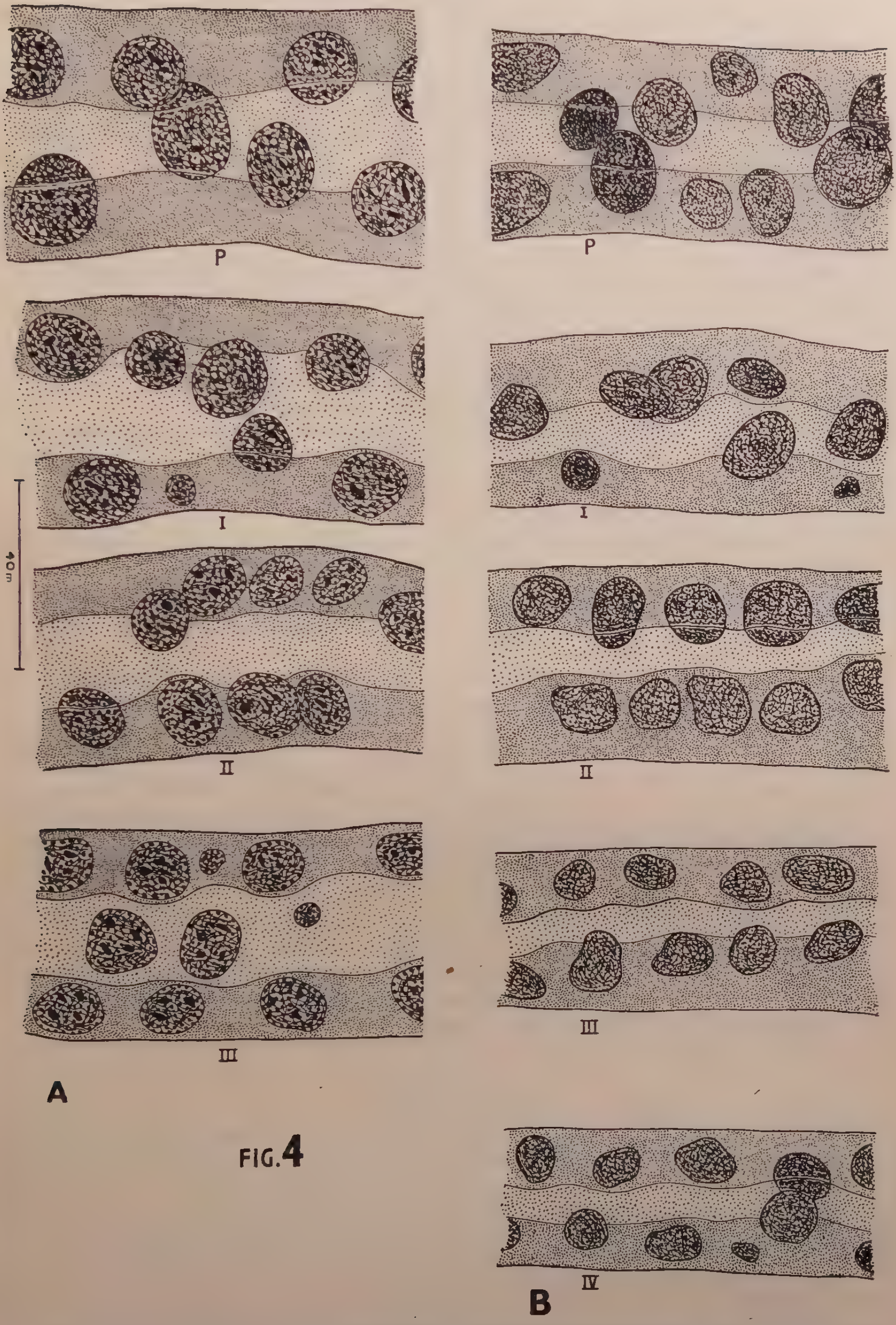

FIG. 4

FIG. 4.—A, the tubules of the fourth instar in surface view; B, the same in the fifth instar (adult). P, I, II, III, IV = the primary and the various secondary tubules.

secondaries added in nymphal instars to form six groups. *Blatta* itself is derived from this type by the suppression of the lateral primaries, and *Forficula* by the suppression of the entire lateral groups and the reduction of the secondaries in the other groups to one per group in each instar. Again one is led to infer that the suppression influence is greater in *Forficula* than in *Blatta* and that the former has closer affinities with the Holometabola than has the latter.

VI. SUMMARY.

(1) *Forficula auricularia* has five instars characterised by the number of antennal joints—8 in the first instar, 10 in the second, 11 in the third, 12 in the fourth, and 14 in the adult.

(2) The Malpighian tubules are in four groups placed dorso-laterally and ventro-laterally at the posterior end of the mesenteron; the region of attachment is expanded to form a definite differentiated basal vesicle.

(3) The tubules are of two kinds; primaries developed in the embryo and secondaries developed in the nymph. The four groups each consist of one primary and four secondaries, the latter being developed in succession, one in each nymphal instar.

(4) Each tubule has upper and lower regions, presumably of different physiological functions, after the manner of *Rhodnius* (Wigglesworth 1931). None of the four primary tubules is associated with the rectum.

(5) The tubules are composed of only two rows of cells, as in the Lepidoptera, not five rows as in *Blatta*.

(6) The secondary tubules arise from an embryonic zone on the posterior side of the basal vesicle, obviously comparable with the similar zone in *Blatta*.

(7) Within a few days of each ecdysis a young secondary tubule becomes visible and passes through the three phases of "cell multiplication," "cell rearrangement" and "cell differentiation." In the first phase the tubule consists of five rows of cells, and growth is by cell division; in the second phase there is no cell division and growth in length is the result of the shifting of the cells on one another until only two rows are present; the third phase occurs at the next ecdysis and consists largely of cell expansion.

(8) At certain ecdyses the diameter of the nuclei of the tubules becomes almost doubled, possibly because of incomplete mitosis which results in a certain degree of polyploidy. This effect does not occur at the first ecdysis; it occurs in all the tubules at the second ecdysis, in the third instar secondaries at the third ecdysis, and in the fourth instar secondaries at the fourth ecdysis.

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WIGGLESWORTH, V. B., 1931, The physiology of excretion in a blood-sucking insect, *Rhodnius prolixus. J. exp. Biol.* **8** : 411–51.

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BOOK NOTICES.

Essays on Growth and Form, presented to D'Arcy Wentworth Thompson. Edited by W. E. Le G. Clark and P. B. Medawar. Pp. viii + 408, 12 pls., portrait, text illust. 8vo. Oxford (Oxford University Press), 1945. Price £1 1*s.* 0*d.*

This volume includes 12 contributions by W. E. Le G. Clark, V. B. Wigglesworth, J. Z. Young, J. H. Woodger, E. C. R. Reeve and J. S. Huxley, P. B. Medawar, Oscar W. Richards and A. J. Kavanagh, N. J. Berrill, E. N. Willmer, J. F. Danielli, W. T. Astbury, and A. J. Lotka. There is, in addition, a list of the published writings of Prof. Thompson by G. H. Bushnell.

D'Arcy Thompson was appointed Professor of Biology in Dundee in 1884, and he still holds the Chair of Natural History in St. Andrews. The essays now published are a tribute to his completion of 60 years as a Professor.

The subject of the essays is one he has made particularly his own, and the papers cover the full range of the subject.

Of particular interest to entomologists is Dr. Wigglesworth's essay on " Growth and Form in an Insect," but clearly the main interest of this book is not in the material used for examples, but the very subject of Growth and Form.

The spell of the Honey Bee. By W. Eric KELSEY. 8vo. London (Chapman & Hall), 1945. Pp. viii + 263, 49 pls., text illust. Price 15*s.*

This attractive book is in three parts : Pt. 1.—The Apiarian Year. Pt. 2.—The Beekeeper's part. Pt. 3.—Nature's consummator.

The first part is concerned with the introduction, the life of the bee in the hive, swarming, the foundation of new colonies and the modern system of beekeeping.

The second part describes the hive and its equipment, the races of honey bee and the many-sided work of the beekeeper. It also includes a chapter on enemies of the bee, and one on bee diseases.

The third part is short, and describes the purpose of the bee, its anatomy, " mental processes," and includes the index.

The book is written by an enthusiastic beekeeper, who has spent much time in lecturing and who learned his apiculture " the hard way." The illustrations are excellent.

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The Publications of the Royal Entomological Society are *Transactions* and *Proceedings.*

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> Smith, A., 1936, New species of Coccidae. *Proc. R. ent. Soc. Lond.* (B) **6** : 301–306, pl. 1.
>
> ——. 1936, New species of Coccidae. *Trans. R. ent. Soc. Lond.* **84** : 901–936.

Titles of periodicals cited are to be abbreviated in the manner indicated in the *World List of Scientific Periodicals, 2nd edition,* 1934.

Authors are entitled to receive 25 copies of their papers free of charge and may purchase additional copies provided that request be made before publication.

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As from January 1936 the journal *Stylops* is continued as *Proceedings Series B. Taxonomy.* Copies of volumes 1–4 are available at *£1 16s. 0d.* each, post free.

MEETINGS

TO BE HELD IN THE SOCIETY'S ROOMS

41, Queen's Gate, S.W.7

1946.

WEDNESDAY, June 5
„ October 2, 16
„ November 6, 20
„ December 4

1947.

WEDNESDAY, January 15 (ANNUAL MEETING)
„ February 5

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

The Fellowship and Fees

Fellows pay an Admission Fee of £3 3*s*. The Annual Contribution of £2 2*s*. is due on the first day of January in each year, and is payable in advance. Fellows under the age of 25 years may pay the entrance fee in three equal annual instalments.

Fees should be paid to the Treasurer, at 41, Queen's Gate, S.W.7, and *not to the Secretary*.

Fellows desiring to pay their Annual Contribution through their bankers may obtain an official form of banker's order by applying to the Treasurer.

Fellows whose Contributions for the current year have been paid are entitled to receive the *Transactions* and *Proceedings* of the Society free of charge. Further copies may be purchased at reduced prices by applying to the Hon. Secretary.

Forms of application for Fellowship, copies of the Bye-Laws and the List of Fellows may be obtained from the Hon. Secretary.

Meetings and Exhibitions

Fellows and others wishing to make a communication to a General Meeting of the Society are requested to send in their names, the title of their exhibit, and a short abstract of their remarks, to the Hon. Secretary fourteen days before the meeting at which it is proposed to make the communication. Should it be desirable to publish a fuller account of the communication the manuscript may be submitted for publication in *Proceedings Series A* or *Series B*. If the epidiascope is required, 24 hours' notice must be given. Objects for projections should not exceed 6 ins. by 6 ins.

Fellows resident abroad, or otherwise unable to attend meetings, are reminded that notes or observations sent to the Secretary may be communicated to a General Meeting on their behalf.

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